

## 13.0 DEALING WITH DENSITY-DEPENDENCE

## 13.1 Introduction

"Density-dependence" is a convenient label for the notion that populations cannot increase in size indefinitely. Eventually some resource becomes limiting and the population tends to level off. In long-lived vertebrates, early survival is often the first parameter to change with increasing abundance. The best known model for a density-dependent response is the logistic equation (eq. 12.12 and 12.26) described in Section 12.3 and 12.5. The resulting curve (Fig. 12.3) shows a smooth approach to an asymptote (usually denoted by  $K$ ). A major problem in applying the logistic equation is that the rate of increase ( $r$ ) declines continuously throughout the growth of the population, approaching zero as the population size approaches  $K$ . This behavior is evident from the underlying differential equation, but is perhaps more conveniently exhibited in the analogous difference equation (eq. 12.25) where it can be seen that

$$r = r_1(1 - \frac{N_t}{K})$$

so that when population size is small relative to  $K$ ,  $r$  is nearly at the maximum value,  $r_1$ , which is sometimes appropriately labeled  $r_{\max}$ .

The logistic curve became popular after Raymond Pearl (1926) used it to describe the growth of yeast populations. While it may be useful as a model for growth of populations of some organisms, the logistic is generally unsatisfactory as a model for growth of populations of large vertebrates. This is because, in practice, the rate of increase tends to be relatively constant over much of the range of population size and then begins to decrease as the asymptotic value is approached. For this reason, a "generalized logistic" curve provides a much more satisfactory model for large vertebrates. For this model,  $r$  holds nearly constant over much of the range of population growth, declining quite steeply as the asymptotic level ( $K$ ) is approached. The generalized logistic is written as a difference equation:

$$N_{t+1} = N_t + r_1 N_t [1 - (\frac{N_t}{K})^z] \quad (13.1)$$

Note the change in notation from  $t-1$  and  $t$  used in Chapter 12 to  $t$  and  $t+1$ . This is done to conform to the notation used in references cited below. When  $z=1$  the rate of increase is as given above, i.e., the rate for the ordinary logistic, written as a difference equation. A comparison (Fig. 13.1) of the two rates of increase (for  $z=1$  and  $z=5$ ) shows why the generalized logistic yields a population growing at a relatively constant rate up until the "carrying capacity" level ( $K$ ) is approached, and is thus a better model for population growth of the long-lived vertebrates, which generally appear to have a relatively constant growth rate at levels below carrying capacity.

In considering density dependence it is important to have in mind some characteristics of different groups of species. Much of the current literature

deals with invertebrates, where very high rates of increase can lead to chaotic-seeming behavior of populations. At the other extreme are the long-lived vertebrates with relatively low growth rates that usually result in less erratic behavior. Many (but not all) species of fish can achieve high growth rates and may thus follow patterns closer to those of invertebrates. Many of the smaller vertebrates have short generation times and thus lack the stabilizing qualities of age-structured populations and can also show substantial year-to-year fluctuations in abundance. Consequently, some of the complexities in the current literature may not be relevant when considering the long-lived vertebrates, and attempts to apply models derived from studies of invertebrates to vertebrate populations may be quite unsatisfactory.

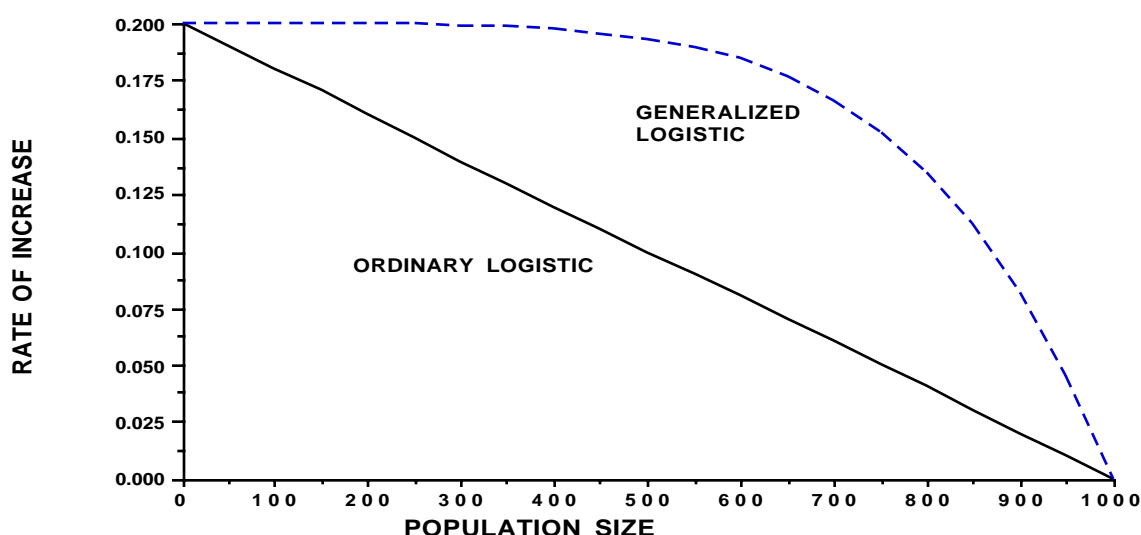


Fig. 13.1 Comparison of rate of increase for the ordinary and generalized logistic growth curves.

Unfortunately, there isn't much in the way of accurate and precise data on population growth in large vertebrates over a wide range of population sizes, making it difficult to demonstrate directly that population growth is more like the generalized logistic curve than the ordinary logistic. However, if one considers Fig. 13.1 and notes that many vertebrate populations do appear to grow exponentially over much of the observed range, the ordinary logistic is much less palatable. Experience with harvested populations also shows that the ordinary logistic will not support observed rates of removals. It is difficult to settle on a value of  $z$ , the parameter governing the rate of decrease in  $r$  with increasing population size. Often one must make an arbitrary choice. In developing guidance for managing cetaceans, the International Whaling Commission considered various values of  $z$ . The value used in various examples here is  $z=5.0$ , which gives the maximum numerical increment of growth at 70% of  $K$ . Because the details of density-dependent responses and "population regulation" are so poorly known for large vertebrates, about all that can be done here is to try to supply some guidance for practical approaches to the subject. The basic assumption is made that populations do not grow indefinitely, and thus are somehow limited.

## 13.2 Some historical aspects

Hairston, Smith, and Slobodkin (1960) produced an all-embracing analysis, starting with the premise that energy is not accumulated significantly in organic matter, and working up from there to conclusions about major trophic levels. Two critiques of their paper then appeared (Ehrlich and Birch 1967, and Murdoch 1966), and were rebutted by the original authors (Slobodkin, Smith, and Hairston 1967). The rebuttal extends the original thesis somewhat and makes for interesting reading. All of these papers depend on qualitative assessment of limiting cases and are thus not very helpful in deciding what controls a specific population. One might, for example, agree that predators as a class are food-limited, without abandoning the notion that particular predatory species seldom increase beyond bounds imposed by behavioral (territorial) constraints.

Andrewartha and Birch (1954) offered the strongest objections to the idea of density-dependence. Various critics of their views emphasized their primary involvement with insects and that many of their conclusions depend on events observed near the geographic limits of particular species, where "limitation by catastrophe" probably does control populations. That this is an over-simplification of their views was vigorously pointed out by both authors, individually and jointly. Some amelioration of the original stand seems evident in later papers by Andrewartha and Birch. In any case, their work has provided useful evidence that many factors may interact to limit populations, not the least of which is the effect of essentially random "shocks" from weather conditions. Murdoch (1994:284) claimed that the "decades-old controversy about regulation has been resolved in recent years", suggesting that the "Nicholson school was right that regulation via stabilizing density-dependent processes is essential to account for species persistence" but that "the local randomness and spatially out-of-phase dynamics emphasized by the Andrewarthan school can create the necessary stabilizing density-dependence".

V.C.Wynne-Edwards promulgated what might be said to be a universal solution -- that social factors, frequently expressed as territorialism, control population size. His thesis closely parallels the wildlife management principle of carrying-capacity, and fits nicely with a readily observed aspect of the behavior of many species. There are, however, too many situations in which territorial behavior does not seem to be either pronounced or effective, perhaps most notable among the larger herbivores. Wynne-Edwards' philosophy is expounded at length in a large book (1962), and compactly in a later paper. Several authors have considered that a weak point in his theme is an invocation of group-selection as a necessary evolutionary device to insure success of regulation by territorialism.

A specific physiological mechanism for population regulation was proposed by J.J.Christian, and then tied to social aspects (Christian and Davis 1964). Objections to the "adrenal function" theory have centered around apparent absence of enlargement of the adrenal glands under situations where it would seem to be called for by the current status or ultimate fate of a particular population. D.Chitty has been particularly explicit on this point (see the discussion and references in Christian and Davis 1964). Chitty's own

attitude on the matter of regulation appeared mostly to have been one of a rather reluctant invocation of a genetic mechanism, at least to handle the problem of cyclic crashes of lemmings and voles. The most detailed exposition of his "polymorphic behavior" mechanism was by one of his students (Krebs 1964) who contrasted that theory with Christian's stress hypothesis and a food-supply hypothesis offered by Pitelka (cf. Pitelka 1958).

One of the apparent reasons for Chitty's belief in a change in quality in vole populations during a decline is the evident necessity for some deleterious factor that persists through more than one generation in order to bring the population down to the low levels observed in the field. In a long-term study of the vole, *Microtus californicus*, Pearson (1966) came to the conclusion that such a factor is supplied by predation. He contended that some other (unspecified) cause is responsible for the initial decline, but that predation then acts to reduce the population to very low levels, whereupon the predators then die off (in the Arctic) or shift to other prey (in temperate regions).

A feature not sufficiently stressed in many analyses of population regulation is that of evolutionary forces. A valuable review of the importance of studying evolutionary ecology is that of Lack (1965). One of his more telling points is that few real opportunities remain to study ecological processes in a sufficiently natural state that one might hope to appraise selective forces free of changes due to human influence.

Even a short excursion into the literature is sufficient to show that there are many views of population regulation. It seems reasonable to suppose that, just as a variety of life forms has evolved, so may have a range of controlling mechanisms. The actual structuring of a population model may, however, call for a specific choice of mechanism, particularly if relatively long spans of time are to be dealt with. On the other hand, if we choose a mathematical relationship to represent population regulation without good evidence that it represents a mechanism actually existing in the population, then we are really deciding the outcomes of the modelling exercise in advance, so that it may have little relevance to the actual population.

### 13.3 Testing for density-dependence

If a population appears to level-off, it may be desirable to have a statistical test to demonstrate that the apparent tendency is not due to chance fluctuations alone. There is a very large literature on testing for density-dependence, but the results are as yet often ambiguous and controversial for large vertebrates. This is perhaps less true for smaller organisms, particularly insects. Due to the very different life histories involved, suitable tests for density-dependence for insects should not necessarily hold for larger species. In particular, most insect populations are capable of very high rates of increase, as are some fish populations. A density-related response may thus occur over a short time span and be readily evident in the data.

One supposed test for density-dependence has been repeatedly shown to be of dubious value over the last 30 years or so, but still turns up in the literature. No doubt this is because the approach is simple and seems natural. It consists of estimating  $\lambda$  from the ratio of two successive population estimates,  $\lambda_t = N_t/N_{t-1}$ , and then calculating the correlation coefficient of  $\lambda_t$  and  $N_{t-1}$  on

a series of such estimates. If  $\lambda_t$  is negatively correlated with  $N_{t-1}$ , then one might assume density-dependence is involved as  $\lambda_t$  apparently decreases with increasing population size. The difficulty, however, is that values of  $N_t$  appear successively in the numerator and denominator of the ratio determining  $\lambda_t$  and this induces a spurious correlation. This prospect was discussed for insects by Watt (1964), and some additional examples were noted by Eberhardt (1970).

There has been considerable interest in testing for density dependence for the last 30-40 years, but it remains uncertain whether density dependence can be reliably detected from a sequence of data on population size or trend alone. Many of the slower-growing populations appear to increase fairly smoothly from low levels, and ultimately show signs of leveling-off. Those with high growth rates may behave quite erratically, making it difficult to discern any pattern. Most of the efforts to devise tests appear to have been inspired by studies of populations showing rather erratic growth patterns, particularly insect populations. Nearly all of the recent efforts proceed along the lines of statistical hypothesis-testing. Most of the available statistical methodology for conducting such tests is based on linear models, and this limits the range of models that can be considered. Most of the tests depend on taking logarithms (base e, usually) of population size, which generally appears to yield symmetrical distributions of deviations from the model, and thus encourages assuming normally distributed errors (a necessary assumption in many of the tests). Statistical hypothesis testing depends on setting up a "null" model and attempting to reject that model in favor of an alternative model. Rejecting the null model does not demonstrate that the alternative model is correct, a fact that sometimes appears to be overlooked in the ecological literature. Because the null model generally needs to be linear and fairly simple in form, the process more or less restricts attention to two models, both linear and quite simple. In some cases, "nested" models may be considered, giving a little more flexibility.

A number of authors have used the following model for density dependence:

$$N_{t+1} = N_t^b K^{(1-b)} \quad (13.2)$$

Where  $0 < b < 1$ , and  $K$  is the asymptotic value. An example of the resulting curve is shown in Fig. 13.2. Taking logarithms gives the model commonly used in studying density dependence:

$$X_{t+1} = bX_t + (1-b)\log_e K \quad (13.3)$$

Here  $X$  denotes the logarithm of  $N$  and  $b$  and  $K$  are as given above. In producing statistical tests, an error term ( $\epsilon$ ), assumed to be normally distributed with some variance is added. Bulmer (1975) wrote the above equation in terms of deviations from  $\mu = \log K$ :

$$X_{t+1} - \mu = b(X_t - \mu) + \epsilon_t$$

Bulmer's is one of the more widely quoted papers on testing for density dependence. He used the null model (described as a "random walk" model:

$$X_{t+1} = X_t + \varepsilon_t$$

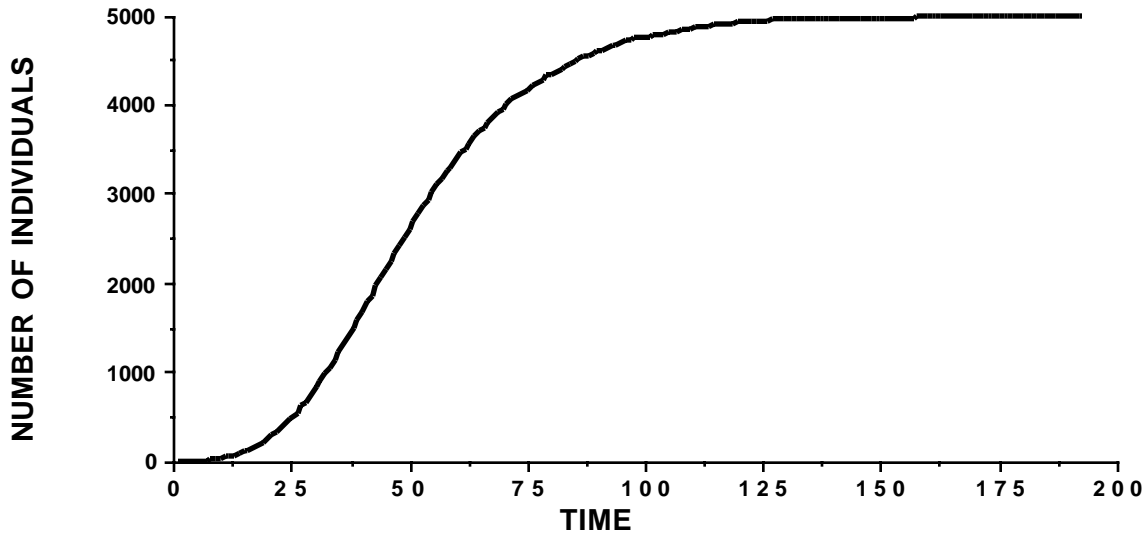


Fig. 13.2 An example of curves represented by Eq. (13.2).  $K=5,000$ ,  $b=0.95$ .

Pollard et al. (1987) used the same models, but added another null model, described as a "random walk with drift":

$$X_{t+1} = X_t + r + \varepsilon_t \quad (13.4)$$

It is important to note that this is the logarithmic form of the usual model for exponential growth (over one unit of time) with a multiplicative error term ( $\varepsilon_t = \log_e e_t$ ):

$$N_{t+1} = N_t \exp(r)e_t$$

Pollard et al. use the three models [one, eq. (13.3) representing density dependence and the two null models above] in "nested" form, so the tests can presumably be used to choose among the 3 models. Examples of the random walk and random walk with drift are shown in Fig. 13.3 and 13.4.

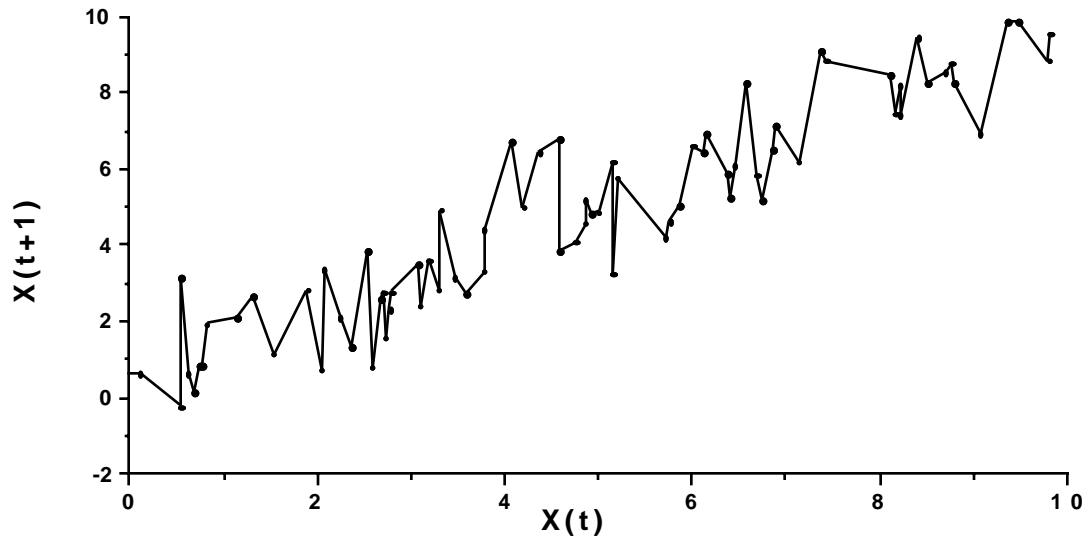


Fig. 13.3 An example of the random walk model used as a null model in various tests for density dependence.

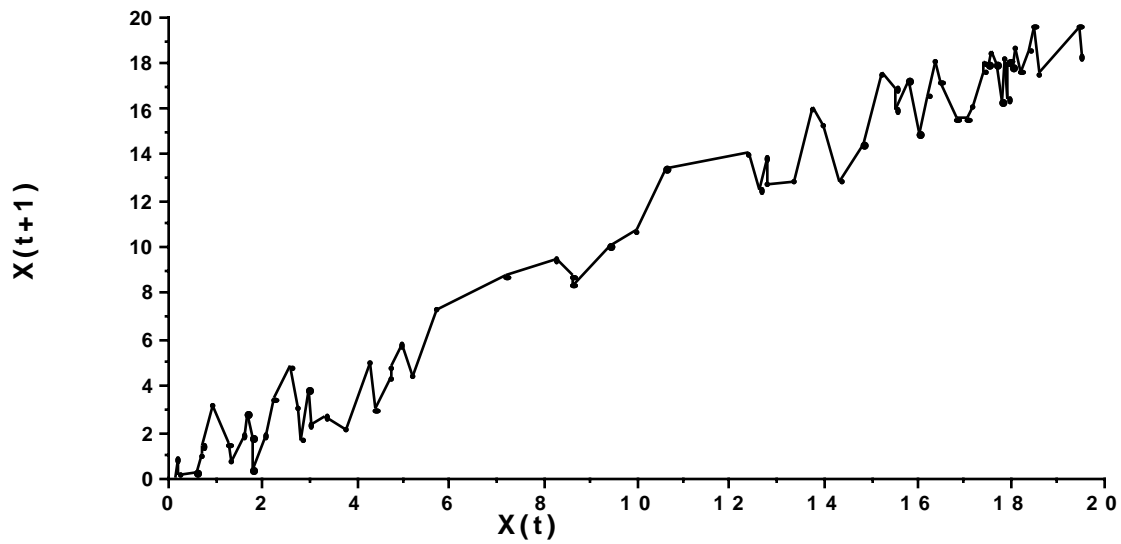


Fig. 13.4 An example of a random walk with drift null model (Eq. (13.4)).

An example of the linear (log scale form) of eq. (13.3) with an additive error term appears in Fig. 13.5.

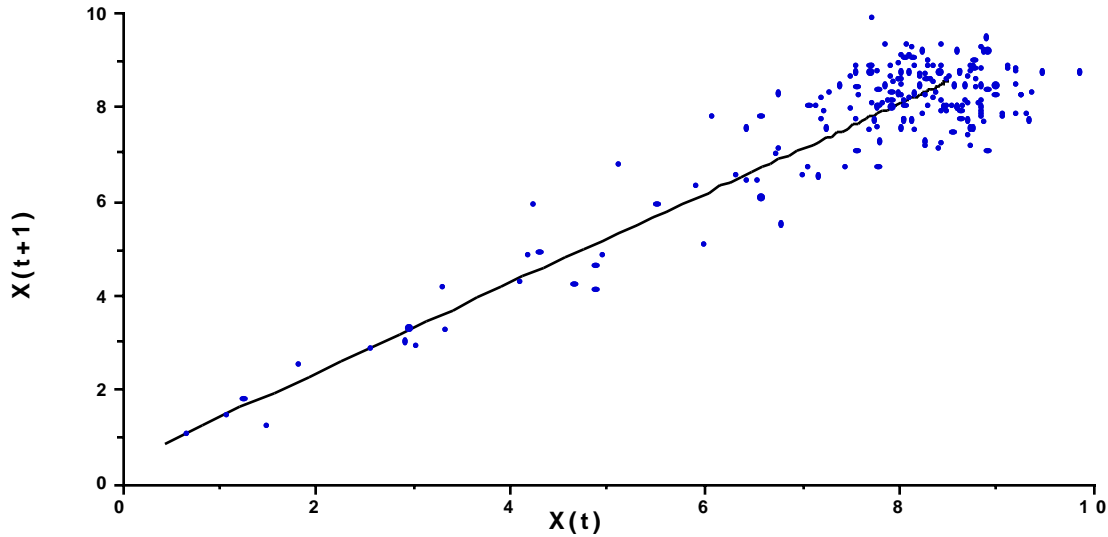


Fig. 13.5 . An example of the linear model of eq.(13.3) with an additive error term

The sizable cluster of points on the right results from the substantial section of the underlying curve (Fig. 13.2 ) close to the asymptotic value.

Some problems with the approach to testing density dependence with the models illustrated above can be seen by comparing the basic model (eq. 13.2) and Fig. 13.2) with the generalized logistic of eq. (13.1). Making such comparisons requires a comparable set of parameters. This can be obtained by choosing parameter values that give similar values of  $\lambda$  for the models of eqs.(13.1) and (13.2). Values of  $\lambda$  for long-lived vertebrates may range up to about  $\lambda = 1.5$  but are often close to 1.2. Rearranging eq.(13.2) gives:

$$\lambda_t = \frac{N_t}{N_{t+1}} = N_t^{b-1} K^{1-b} = \left(\frac{K}{N_t}\right)^{1-b}$$

and values (Fig. 13.6) of  $b=0.95$  and  $b=0.98$  fall in this range (up to  $\lambda = 1.5$ ). Comparing the generalized logistic with these two curves (Fig. 13.7) shows the sharp difference between eq.(13.1) and eq. (13.2). Using smaller values of  $b$  shifts plots of eq. (13.2) to the left but yields the much larger values of  $\lambda$  characterizing insects and some species of fish.



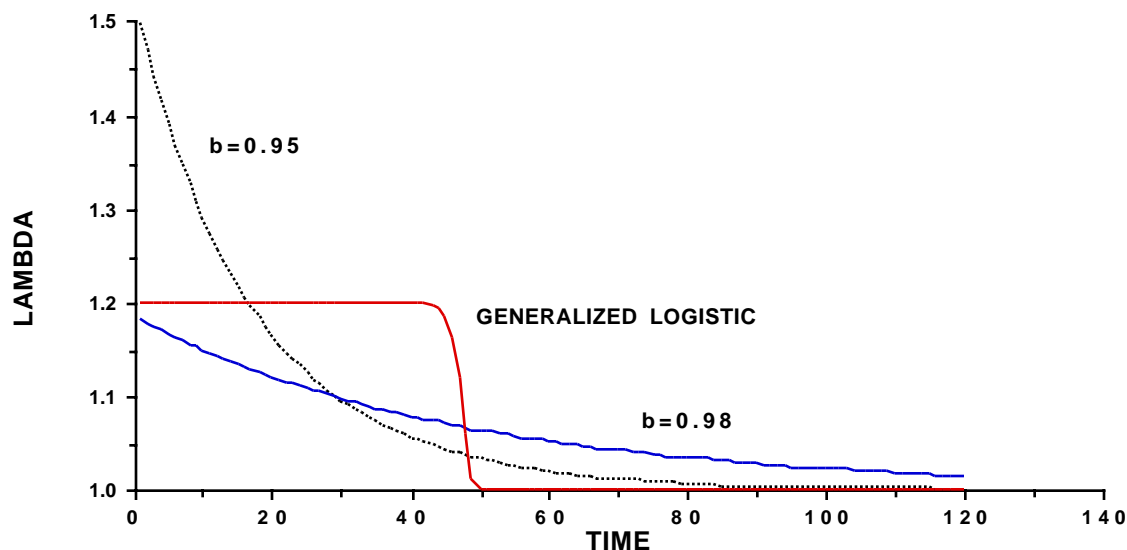


Fig. 13.6 Lambda for density dependence model used by Bulmer (1975) and Pollard et al. (1987) compared with lambda for a generalized logistic curve. Values of  $b$  used here are much larger than those encountered in studies of invertebrates in order to obtain values of  $\lambda$  in the range expected for long-lived vertebrates.

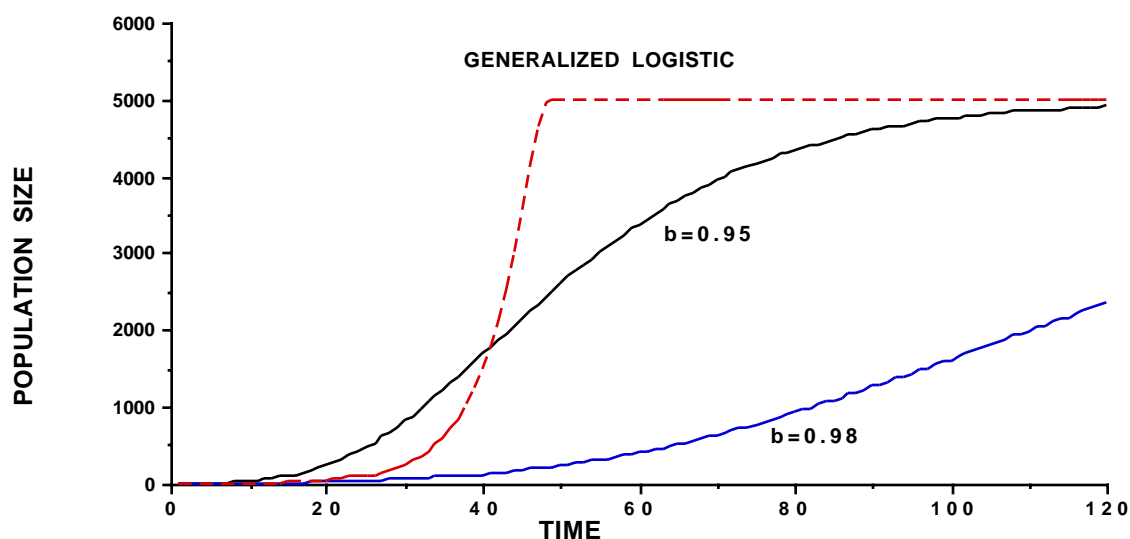


Fig. 13.7. Comparisons of curves from eq. (13.1) and a plot of the generalized logistic (broken line above). Generalized logistic curve based on lambda 1.2 and  $z = 5.0$ .

A basic issue thus is that the curves are quite different, so that there may be a question about efficiency of the test if the alternative model really should be more like the generalized logistic than like eq.(13.1). Another important issue is that the generalized logistic curve behaves essentially as an exponential curve for the lower part of its range (see Fig. 13.1), so one would expect that the null model of eq. 13.4 would not be rejected for a population growing in the lower part of its range. Thus the test would have essentially zero power of detecting density dependence in an important portion of the

range of growth. This is not necessarily true for eq. (13.2) as  $\lambda$  is large and changes dramatically in the early growth phase for smaller values of  $b$ . Hence the tests may be effective for insects and fail for long-lived vertebrates.

Dennis and Taper (1994) proposed tests for a more complex model of the following form:

$$N_{t+1} = N_t \exp(a + bN_t + \sigma Z_t) \quad (13.5)$$

where  $b < 0$  and  $Z_t$  is assumed normally distributed with zero mean and unit variance, while  $\sigma$  is a constant that lets one choose the variance of the error term. Taking logarithms gives:

$$X_{t+1} = X_t + a + b e^{X_t} + \sigma Z_t \quad (13.6)$$

This model is thus nonlinear (because of the exponential term), making for “intractable” distributions of test statistics. Dennis and Taper got around the problem by using bootstrapping and some simulations to check their results. The model of eq.(13.5) is equivalent to one used by W.E. Ricker (1975) to study stock-recruitment in fish [essentially the relationship between size of a parental generation (stock) and the succeeding generation (recruits)]. Without the error term, eq.(13.5) can be written as:

$$N_{t+1} = N_t e^{r(1 - \frac{N_t}{K})}$$

where  $r$  is the growth rate and  $K$  is the asymptotic value. If  $r$  is in the range of growth for most long-lived vertebrates (say  $0 < r < 0.5$ ) then a good approximation to the above curve can be obtained by using the first two terms of the Taylor series expansion of the exponential term above, obtaining:

$$N_{t+1} = N_t + rN_t(1 - \frac{N_t}{K})$$

which is the discrete form of the logistic growth curve (more details are available in Eberhardt 1977). This brings the model of Dennis and Taper (1994) closer to the kind of growth curve one might expect would hold for long-lived vertebrates. However, they also use nested models with the same random walk and random walk with drift (eq. 13.4) used above. Hence, if the generalized logistic actually is the best model for a given population, then the power of the test for populations at the lower end of the growth range is again essentially zero, as discussed above.

Further difficulties with the recent approaches to testing for density dependence were proposed by Shenk et al. (1998) who used computer simulations designed to mimic the incorporation of sampling error in the data. In most assessments, the error term is assumed to be due to “changes in climate and other environmental factors” (Bulmer 1975), although Bulmer did consider sampling error in one of his tests. Shenk et al. concluded that

“because these tests have been shown to be either invalid when only sampling variance occurs in the population abundances (Bulmer’s  $R$ , Pollard et al.’s and Dennis and Taper’s tests) or lack power (Bulmer’s  $R^*$  test), little justification exists for use of such tests to support or refute the hypothesis of density dependence”. It seems likely that their results will not be the last word on the issue, inasmuch as it is possible to estimate the contribution of sampling error in at least some circumstances, and also because they chose to use a model of a large mammal population to simulate density dependence in their analyses, while most of the methodology described above seems most appropriate for insect populations.

Only a brief sketch of apparent problems in testing for density dependence has been attempted here. Clearly the suggested difficulties need to be examined in more detail. This calls for assessments of the actual tests and thus brings in the subject of likelihood ratio testing.

### 13.4 Population regulation

A broader view of the issues involved in testing for density dependence was taken by Murdoch (1994). He discussed population regulation, “which arises as a result of potentially stabilizing density-dependent processes, even when brought about by ‘non-equilibrium’ mechanisms”. He defined regulation very broadly, stating “Population regulation seems best defined by defining non-regulation, which is random walk dynamics”. He defined random walk in the form described above as random walk with drift” (eq.13.4) and thus espoused the null model of exponential growth. Such a population is unbounded (i.e., increases indefinitely) and thus Murdoch stated that “we can identify regulation with boundedness”. Because nearly all populations (excepting perhaps humans) appear to be bounded, practical-minded observers may see little reason to study density dependence. However, Murdoch suggested several possibilities for modes of population change that may transcend the simpler concepts of density dependence. He noted that regulated populations “thus include not only those with a stable equilibrium but also those with a stable attractor, i.e., cyclic or chaotic populations”. A cyclic model was described here by eq.(12.33) and (12.34) and illustrated in the upper panel of Fig. 12.4. Another very interesting concept for regulation without apparent density dependence can be developed by considering a metapopulation in which isolated subpopulations follow a random walk (without “drift”) and ultimately go extinct but with the area they occupied later recolonized by immigration from another distinct population. Murdoch (1994:275) commented that “little can be inferred from a statistical analysis of the time series of a single population. Thus if we are interested in exploring regulation in a particular population we need to investigate the mechanisms directly.”

Murdoch (1994) reported the results from assessments of a large number of sets of data on small bird populations that found the populations to be remarkably stable. He commented that “The remarkable invariance of these bird populations makes it difficult to believe that they are not in fact well regulated. If they are, we clearly have still not developed adequate means of detection”. From a statistical point of view, there is little or no prospect of detecting tight regulation from an analysis of the time series of observations alone. This is essentially proposing to prove a null hypothesis holds, when we can only reject a hypothesis through statistical analysis. Another example of

this problem concerning an elk population is discussed in Section 14.6 . In that example there is good evidence of a strong climatic effect that results in dramatic changes in first-year survival, yet the population trend is far less variable than would be expected. Our tentative conclusion is that high survival of adults “buffers” the effect of variable first-year survival, and that there is a strict upper limit on first-year survival enforced by the availability of winter thermal refugia. Examination of population trends can only show that there is much less population variability than one would expect on the basis of environmental data (30 years of snow depth data are available) so that the main prospect for assessing density effects is by direct measurement of population parameters. Detecting regulation then requires that the populations somehow be perturbed and essential parameters monitored during the return to an equilibrium condition.

### 13.5 Testing for a maximum net productivity level.

Thus far we have seen that the prospects for detecting density dependence from a series of measurements of population trend are presently doubtful. In the present section, we assume that density dependence does prevail in a population and seek a means to determine how it affects the current trend. An important practical problem is to determine status of a population with respect to the maximum net productivity level (MNPL). This is the point where the slope of the s-shaped curve of population growth shows a change in rate of change of the slope (the inflection point of the curve). Determining status of a population with respect to this level is important for several reasons. One is that the maximum sustainable yield (MSY) of a population can be taken at this level, a second is that this point figures in legislation that requires managing populations at or above that level (for example, the Marine Mammal Protection Act of 1972), and a third is the evidence (suggested in Section 13.3) that there likely is little prospect of detecting density dependence using the approaches presently in the literature when a population is below the inflection point in the growth curve. It is important to stress that the test suggested here depends on assuming that an s-shaped growth curve does govern the trend of a particular population, i.e., that we assume density dependence exists.

The basis for the test is to attempt to ascertain whether the recent trend of the population traces out a curve that is concave upwards (below MNPL) or concave downwards (above MNPL). This approach thus assumes an s-shaped growth curve and the existence of density dependence. The test has two stages and depends on the approximate test for curvilinearity given in Section 1.7. In the first stage, a straight line and second degree polynomial are fit to untransformed data. If the test for curvature is significant, we conclude that the population is below MNPL. If the test is not significant on data in the arithmetic scale, then we transform to the log scale and repeat the test. Significance suggests the population is above MNPL. The test was studied with simulations based on the assumption that the generalized logistic applies to first-year survival according to eq. 13.7.

$$s_1 = s_0 \left[ 1 - \left( \frac{N_t}{K} \right)^z \right] \quad (13.7)$$

Here  $N$ ,  $K$ , and  $z$  are as before and  $s_0$  is a constant while  $s_1$  denotes first-year survival. This general approach was later used in the simulations of Shenk et al. (1998). More details on the test and simulation are available in Eberhardt (1992). The approach essentially depends on the fact that the usual growth curve is concave upwards below MNPL and concave downwards above MNPL. However, transformation to the logarithmic scale yields a curve that is nearly a straight line below MNPL but remains concave downwards above that point (cf. Eberhardt 1992:Fig. 3), and this seemed to improve the power of the test (Eberhardt 1992).

### 13.6 Components of density dependent responses

If, as seems to be the case generally, one cannot reliably detect density dependence from a sequence of measurements of population trend data, it will be necessary to examine the behavior of population parameters as the population changes. Thus far there are relatively few sets of data that provide the necessary details. Some preliminary results can, however, be suggested. It appears to be a generally accepted principle that adult female survival is the key to well-being of at least the populations of the long-lived vertebrates, and quite possibly to most of the sexually reproducing species. Over 20 years ago it was proposed that there appears to be a sequence of changes in vital rates as population density increases towards maximal levels (Eberhardt 1977). Later studies support this sequence (Fowler 1981,1987, Gaillard et al. 1998). The proposed sequence is given in Fig. 13.8.

With the advent of effective mark-and-recapture methods, particularly those employing radiotelemetry, it has become possible to obtain data on this sequence for a number of large mammal populations, and to estimate the rate of change ( $\lambda$ ) from such data. Often the resulting estimate of  $\lambda$  can be checked by direct estimates of population density over time, or through measures of relative abundance (indices of abundance). Inasmuch as most estimates from field data are subject to a variety of potential biases, it is very important to have estimates from both reproductive and survival data and from independent direct measures (census or index).

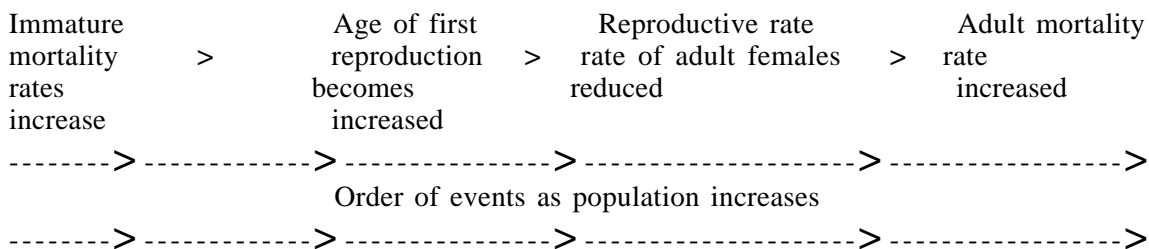


Fig. 13.8 Sequence of events contributing to regulation as a population of long-lived vertebrates increases in abundance.

For populations with little impact of human activities, adult female survival appears likely to be at least 0.94 and likely higher (Fig. 13.9). Many of the examples used here were subjected to impacts that likely reduced survival below a feasible maximum. Consequently, it seems very likely that adult female

survival will be at least 94% and may be 99% or higher in the prime age classes under truly undisturbed conditions. Such a high annual survival is necessarily accompanied by reductions in survival due to senescence which may not always be taken into account in reported estimates of adult female survival.

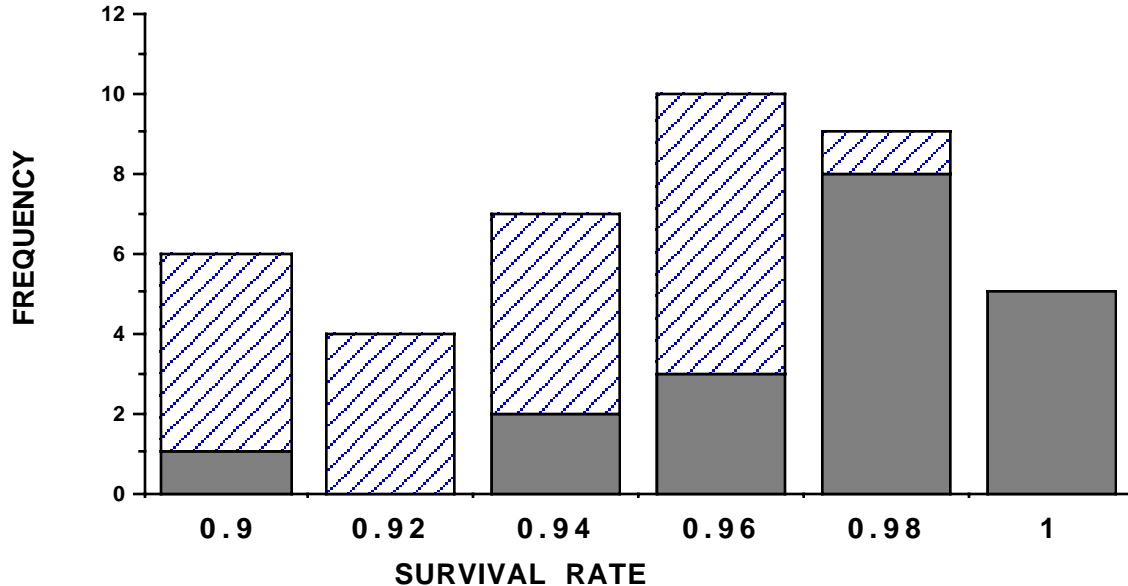


Fig. 13.9. Frequency of adult female survival rates. Most of the examples are from large mammal data, but a few are from long-lived birds. Dark bars represent species where there is reason to believe human influence might have a minor influence, while those represented by the lighter bars likely were affected by modest human influences.

Under largely undisturbed conditions, it seems reasonably well-established that a density-dependent response in long-lived vertebrates will initially be evident in first-year survival. Poor first-year survival normally results in poorer physical condition which will, in turn, result in a delay in ages of first reproduction. It may well be that these two factors will be sufficient to control population growth without invoking the subsequent stages of Fig. 13.8, but extreme conditions may well result in an impact reflected in all four stages. The Hawaiian monk seals of French Frigate Shoals provide one example of this result (Section 14.5 and Example 13.1 below).

In Chapter 11 (Section 11.9) we considered a method for obtaining approximate variance estimates for the rate of population change ( $\lambda$ ). An essential component is estimating the partial derivatives of  $\lambda$  with respect to survival and reproductive rates (eq. 11.13). These provide a measure of the relative importance of such rates in determining population growth. They indicate that adult female survival is most important, with reproductive rate next, and survival to reproductive age apparently least influential (Fig. 13.10). We can thus speculate that, because long-lived vertebrates have relatively slow rates of population growth, early survival might be the best mechanism for at least initiating population regulation.

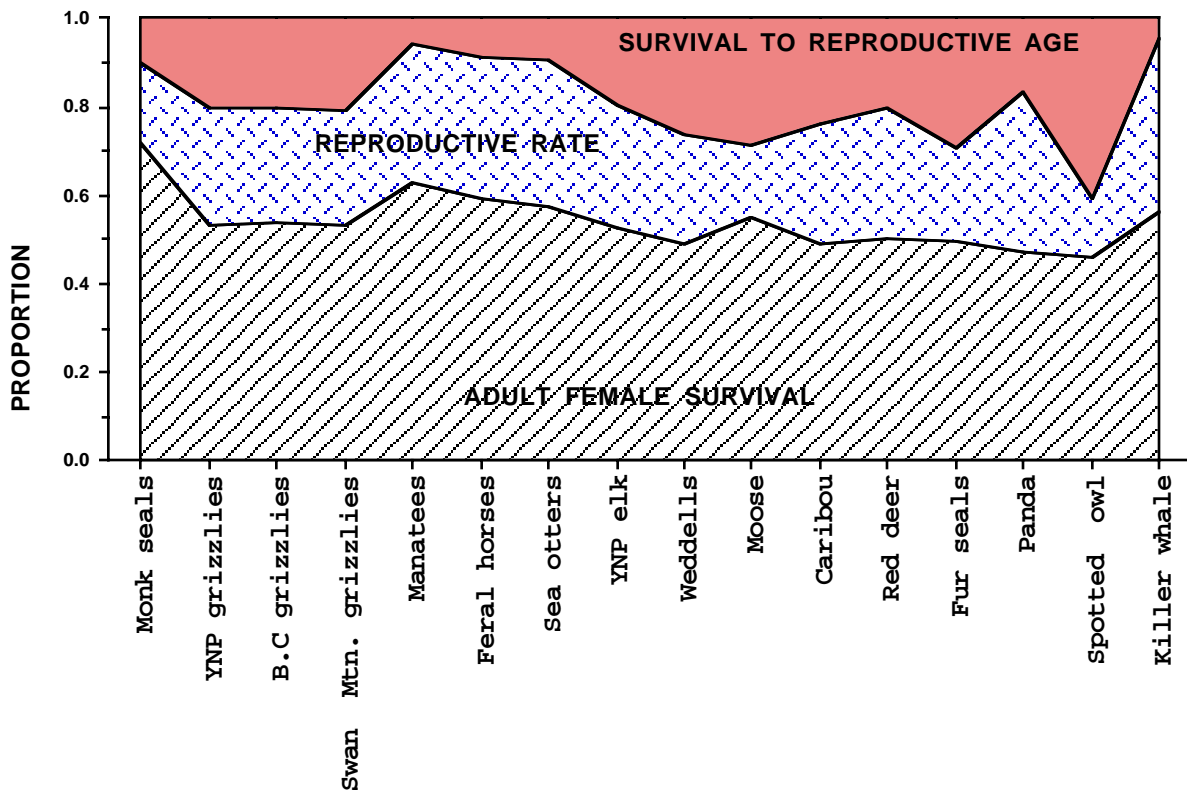


Figure 13.10 Relative importance of components of rate of population change for a number of species of long-lived vertebrates.

The evidence for reduced juvenile survival as the first parameter to change with increasing population density is now quite substantial. Gaillard et al. (1998:Table 1) reported that juvenile survival was implicated in 7 of 8 species for which there was evidence of density dependence. They noted that Fowler's (1987) review showed juvenile survival involved in 15 of 21 species for which density dependence was reported. A major problem in assessing data from the literature is that the chronological sequence in which various parameters change often cannot be determined from the reports, but it does seem clear that changes in the age of first reproduction largely follow as a consequence of the reduced resource availability leading to reduced early survival.

Gaillard et al. (1998) presented data that showed much greater relative variability (coefficient of variation) in juvenile survival (their Table 3) as contrasted to that of adult female survival (their Table 2). The likely cause of the higher variability in juvenile survival was illustrated by Gaillard et al. (1998:Fig. 1) as the sequence in time of adult female and juvenile survival

rates. As density increased, juvenile survival decreased sharply, thus substantially increasing the coefficient of variation. Gaillard et al. (1998) noted that "only two island populations (Soay sheep and red deer) exhibited density dependence in adult survival" and that "Even for these two species, survival of adult females varies much less than juvenile survival." Discussing red deer, Saether (1997) pointed out that "the major density dependent mortality losses occur among calves during their first winter", and that "This pattern was found in three different studies of the species in both Europe and North America". Gaillard et al. (2000) reviewed a substantially larger set of data that confirmed the results of Gaillard et al. (1998) and ranked variability from highest in juvenile survival to lowest for adult survival.

Clutton-Brock et al. (1991) reported that "The persistent instability of the St. Kilda [Soay] sheep population is probably caused by their consistently high fecundity associated with a super-abundance of food in summer. In conjunction these may permit the population to pass through winter at a level close to carrying capacity; to increase as much as 50% during the subsequent summer; and to enter the next winter at a level substantially higher than the island can support".

A major problem in assessing the sequence proposed here is the uncertainty as to the forces that regulated undisturbed populations before human interference became all-pervasive. The relative magnitudes of the numerical values of the essential parameters (Fig. 13.10) indicate that "sensitivity" of  $\lambda$  to parameter changes is least in early survival and greatest in adult survival, with reproductive rate in an intermediate position. It might thus be supposed that this sequence may have some significance in an evolutionary sense. The notion of "r and K selection" has lost some of its earlier preeminence, but nonetheless provides a convenient shorthand classification of species, with r-selected groups able to recoup losses in a very short period, and K-selected species requiring many years to recover from reductions in numbers. Consequently, it seems logical that selection in K-selected species might favor a regulatory process that tends to maintain equilibrium numbers by small, rather than large, changes in  $\lambda$ , hence by modifying early survival. This argument is supported by the results of Gaillard et al. (2000) who evaluated temporal variation in "fitness components" of large herbivores. These authors found that the coefficient of variation for early survival was highest (0.64) in large herbivores and lowest for adult survival (0.09). They suggested that "the immature stage ... may be the critical component of population dynamics for large herbivores", indicating that "our review supports Eberhardt's hypothesis and generalizes it to all sources of temporal variation".

Three major forces can be proposed as influencing the large vertebrates under "natural" conditions: weather, resources and predation. The preponderance of evidence from demographic studies indicates that early survival responds first to both severe weather and to resource limitations. As a population begins to outstrip its resources, inclement weather may have a much more pronounced effect, and may result in rather sharp fluctuations. A key question is the possible regulatory role of predation. In most natural systems human interference severely limits opportunities to evaluate the role of predation (Section 12.5). Wolf (*Canis lupus*) predation on ungulates has been observed to dominantly affect early survival and survival of senescent individuals (Peterson 1977, Peterson et al. 1984:Fig. 5, Ballard et al. 1987:Fig. 16,



Mech et al. 1998). To serve as a regulatory function, predation should exhibit a direct relationship with prey density, increasing at high prey densities and decreasing at lower prey numbers. The notion of ratio dependence (Matson and Berryman 1992) may fulfill this requirement. Evidence has accumulated to favor the ratio dependence model in wolf-ungulate interactions (Eberhardt 1997, 1998). The crucial question may then be whether predation tends to hold ungulate populations below levels where weather and resource limitations become important. If so, then an evolutionary pattern may be implicated.

Example 13.1 Sequence of events in density dependence.

The illustration of the original development (Eberhardt 1977:Fig. 2) of the sequence of events indicated in Fig. 13.8 used data from a number of sources. The Hawaiian monk seal population of French Frigate Shoals (Section 14.5) illustrates the full sequence in a single population. Trend of the French Frigate Shoals population through 1993 appears in Fig. 1.18, and was contrasted with the other sites by Gilmartin and Eberhardt (1995). The population increased steadily until sometime in the 1980's, and then began a dramatic decline. The decline was initially evidenced by finding malnourished pups, and a decreasing first-year survival (Fig. 13.11).

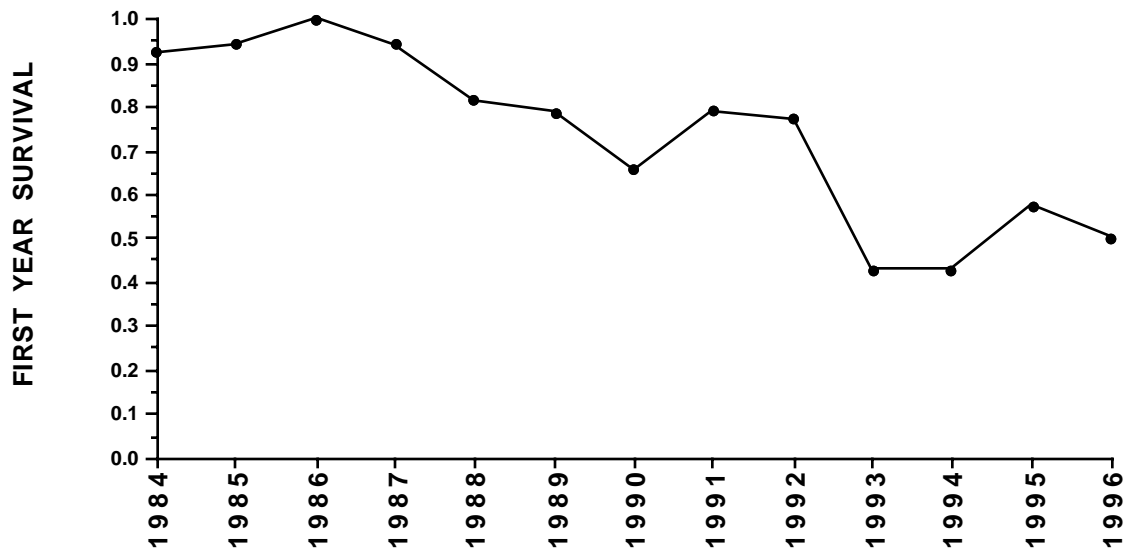


Fig. 13.11 First year survival of monk seals on French Frigate Shoals.

High adult survival was recorded during the phase of population increase (Gilmartin et al. 1993), but soon began a steady decrease. The population is not a large one, so the number of weaned pups tagged each year (a major effort is made to tag all pups at weaning) has averaged around 40 individuals. Consequently sample size has an appreciable effect on the numbers of older animals located (less than 10 individuals in the data used here), as does the stochastic (chance) variation in survival. Nonetheless, the pattern of decreasing survival is very evident in logarithmic plots of numbers observed over the years (Fig. 13.12).

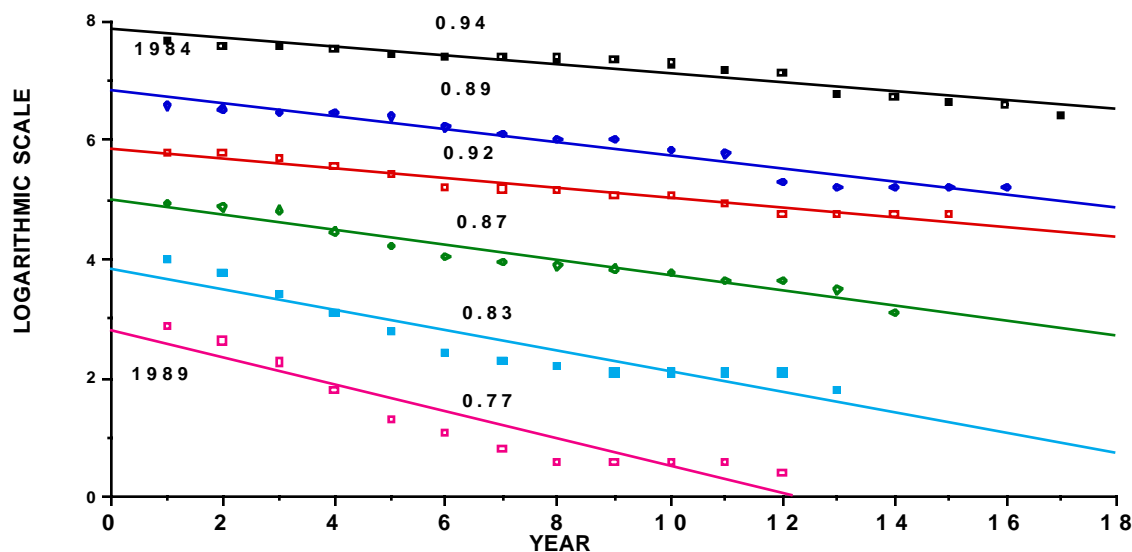


Fig. 13.12. Logarithms of numbers of tagged seals recorded at French Frigate Shoals, Northwest Hawaiian Islands, 1984 through 1989. Estimates of survival rates are shown for each year-class. Because the numbers initially tagged (as weaned pups) are roughly the same, the vertical scale has been adjusted so that the points do not overlap.

The survival rates given in Fig. 13.12 were obtained from the slopes of logarithms of numbers of individuals returning to the Atoll each year. More details on survival estimation appear in Gilmartin and Eberhardt (1995). It appears that there has been a steady decrease in adult survival rates, and this is, of course, evident in the population trend (Fig. 1.18). It is particularly interesting that the first cohort tagged (1984) apparently continues to have relatively good survival. The decreasing trend in survival rates has continued, so that the cohort tagged in 1996 exhibits an annual survival rate on the order of 40%. Evidently the available food resource for this population has continued to decline, and "carrying capacity" may not yet have been reached.

Due to relatively small sample sizes, it has not been feasible to determine whether the sequence of events of Fig. 13.8 has occurred in this population in precisely the order suggested, but clearly the prescribed series of events has transpired. Age of first reproduction clearly has been reduced, and it seems reasonably certain that the overall reproductive success of adult females has decreased (Fig. 13.13). The oldest tagged individuals in the overall population are now about 18 years of age, so it is as yet to be determined when senescence becomes important. The largest sample of reproductive data comes from another site (Laysan Island, see map in Section 14.5), and suggests that monk seals do not reach a reproductive peak until appreciably later than other pinnipeds.

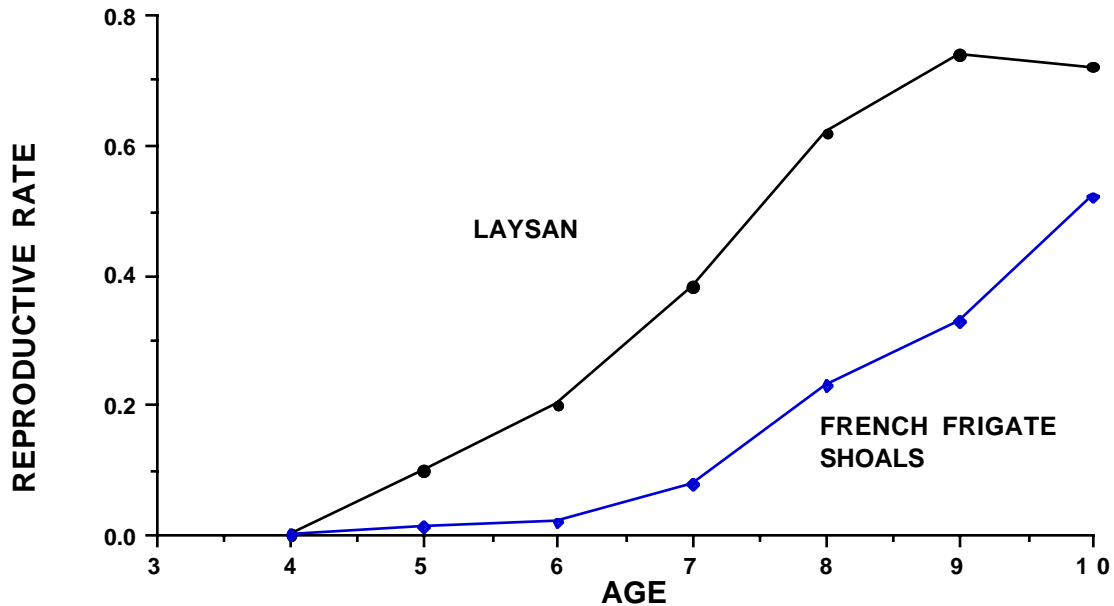


Fig. 13.13 Reproductive rates for monk seals at Laysan Island and French Frigate Shoals.

It should be noted that this example very likely is not typical, in the sense that there is not sufficient information to determine what the "typical" approach to an asymptotic population level might be. As noted previously in this Chapter, it may be that a reduction in first year survival and the (likely) concomitant delay in first reproduction may be sufficient to cause a population to stabilize in the neighborhood of a carrying capacity value. This is one of the issues that characterize the limitations of the present state of knowledge about long-lived vertebrates.

### 13.7 Exercises

13.7.1 Make plots of the rate of increase used in Eq. (13.1) and Fig. 13.1 for  $r(1)=0.2$ ,  $z=1,2,5,11$ , and  $K=5000$ .

13.7.2 A model for density dependence.

Plot eq.(13.3) with  $b=0.95$  and  $K=5000$  and the log form of the generalized logistic [eq.(13.1)] with  $r(1)=0.2$ ,  $z=5$ , and  $K=5000$ . Note that you will need to rearrange eq.(13.1) to put it in a log form, and that you will need to use  $\exp(\ln X(t))$  to represent  $N(t)$  in the portion of eq.(13.1) in brackets, inasmuch as  $\exp(\ln(x))=x$ .

13.7.3 Generating normal distributions.

A convenient way to generate normally distributed errors for studying density dependence is given in the following equations:

$$x_1 = (-2 \log_e r_1)^{1/2} \cos 2\pi r_2$$

$$x_2 = (-2 \log_e r_1)^{1/2} \sin 2\pi r_2$$

where the  $x$ 's are random normally distributed values with mean 0 and variance 1 and the  $r$ 's are uniform random variables (range 0-1). You can obtain uniform random variables with the function `RAND()` in EXCEL (note that you need the parentheses to generate uniform random variables but don't

need to enter a value in them). The above equations generate 2 random normal variables from 2 uniformly distributed values. In doing largish simulations its convenient to use both of the random normal numbers thus generated. For purposes of illustration, we need only use one. Set up a table of random normal numbers using the above equations and try the random walk of Fig. 13.3, using 100 values. Create a graph on the same EXCEL sheet and change the values to see how the random walk changes. Note that the populations go extinct fairly regularly, whereas Fig. 13.3 shows an increasing population. EXCEL has a command that changes the random numbers to make a new graph. on occasion it is desirable to make the recalculation manual so as not to have the graph change while you are working on it.

#### Exercise 13.7.4 “Random walk with drift”.

Several of the papers referenced in this chapter discuss “random walk with drift” using eq.(13.4). It was noted in connection with eq.(13.4) that this really simulates an exponentially increasing population. Add another column to the random normal numbers generated above which multiplies one of the random normal numbers by a constant so that you get an error term like that used in eqs.(13.5) and (13.6). Then add a constant to the random walk model above to construct results according to eq.(13.4), as shown in Fig. 13.4. Make a graph of the random walk model on the same EXCEL sheet. Vary the constant multiplying the normal random variable from, say, 0.1 to 1 and note how it affects the graph of population size. With a small multiplier the graph should essentially follow an exponential plot (but on a log scale). With a larger multiplier it becomes quite erratic.

#### Exercise 13.7.5 Rapid rates of increase.

It was noted in the Chapter that many of the papers on testing for density dependence appear to be based on data on insects. To examine this prospect, plot eq.(13.2) as shown in Fig. 13.2 with  $K=5000$ , but set it up with 3 columns and make a graph so you can compare different values of  $b$ . Try  $b=.95$ , and  $b=.98$  which should replicate Fig. 13.2 and part of Fig. 13.7. Now try values of  $b=0.5$  to  $0.8$  to see how different the growth curves are.

#### Exercise 13.7.6 Lambda for rapid rates of increase.

Add 3 columns to the worksheet for Exercise 13.7.5 to show lambda for each of the population plots. This can be done with the equation given in the chapter, i.e.

$$\lambda_t = \frac{N_t}{N_{t+1}} = N_t^{b-1} K^{1-b} = \left(\frac{K}{N_t}\right)^{1-b}$$

This shows why the growth curves of exercise 13.7.5 increase so rapidly.

#### Exercise 13.7.7 The generalized logistic.

Calculate the generalized logistic (eq.13.1) for  $K=5,000$ ,  $z=5$ ,  $r=0.2$ ,  $0.4$ , and  $K=5,000$ ,  $z=2$ ,  $r=0.2$ ,  $0.4$ , and make a graph of the results on the same worksheet. Note the more rapid increase generated by  $r=0.4$ . One characteristic of the generalized logistic is shown by the “overshoot” and oscillation for higher rates of increase and larger values of  $z$ .

## Exercise 13.7.8 Bulmer's tests

Some of the difficulties in testing for density dependence can be illustrated by considering Bulmer's (1975) tests. The first test is based on the fact that the squared differences between successive observations of population size can be used to approximate the overall variance of a set of observations, if there is no trend or pattern in the data. The test is essentially the Durbin-Watson test of eq. (9.13), except that Bulmer used the reciprocal of the ratio, i.e., the reciprocal of eq.(9.13). The table below gives the first 20 observations from the generalized logistic used in Exercise 13.7.2, 20 observations bracketing the inflection point, and 20 observations above the inflection point, along with logarithms of 20 observations from an exponential growth curve with  $N(0)=10$ ,  $r=0.20$ .

First 20 obsns generalized logistic				
		5 OBSNS 0.2 BRACKETING 5000 INFLECTION 10 POINT	OBSNS ABOVE INFLECTION POINT	EXPONENTIAL MODEL N(0)=10 R=1.2 X(t)
X(t)		X(t)		
1	2.30259	7.04288	8.51718	2.30259
2	2.48491	7.22509	8.51719	2.48491
3	2.66723	7.40715	8.51719	2.66723
4	2.84955	7.58883	8.51719	2.84955
5	3.03187	7.76954	8.51719	3.03187
6	3.21419	7.94789	8.51719	3.21419
7	3.39651	8.12049	8.51719	3.39651
8	3.57884	8.27961	8.51719	3.57884
9	3.76116	8.40979	8.51719	3.76116
10	3.94348	8.48962	8.51719	3.94348
11	4.12580	8.51505	8.51719	4.12580
12	4.30812	8.51718	8.51719	4.30812
13	4.49044	8.51719	8.51719	4.49044
14	4.67277	8.51719	8.51719	4.67277
15	4.85509	8.51719	8.51719	4.85509
16	5.03741	8.51719	8.51719	5.03741
17	5.21973	8.51719	8.51719	5.21973
18	5.40205	8.51719	8.51719	5.40205
19	5.58437	8.51719	8.51719	5.58437
20	5.76669	8.51719	8.51719	5.76669

Bulmer's first test is  $R=V/U$  where:

$$U = \sum_{i=1}^{n-1} (x_{i+1} - x_i)^2 \quad \text{and} \quad V = \sum_{i=1}^n (x_i - \bar{x})^2$$

He gives a way to calculate significance levels, which gives a value of 0.696 for the 1 % point and 0.909 for the 5% point, where the test is significant if the R is less than the stated significance point. Calculate Bulmer's R test for the first three columns above and comment. Also comment on the meaning of a comparison of the first and last columns (note that the data are available in your results for Exercise 13.7.2 so you don't have to copy the numbers above).

Exercise 13.7.9. Bulmer's second test.

Bulmer (1975) recognized that his R-test would not behave satisfactorily in the presence of sampling error so devised a second test for that purpose, which is  $R^*=W/V$  where:

$$W = \sum_{i=1}^{n-2} (x_{i+2} - x_{i+1})(x_i - \bar{x})$$

He gives approximate criteria for significance as:

$$R_{0.05}^* = -\frac{13.7}{n} + \frac{139}{n^2} - \frac{613}{n^3}$$

$$R_{0.01}^* = -\frac{20.1}{n} + \frac{258}{n^2} - \frac{1279}{n^3}$$

and indicates significance if  $R^*$  is less than the calculated significance level. Try this on the first 20 observations for the generalized logistic as given in Exercise 13.7.8 and comment on your results.